Recent tree-limit history of *Picea abies* in the southern Swedish Scandes

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The recent history of *Picea abies* (L.) Karst. at its altitudinal tree limit has been studied in the southern Swedish Scandes. Altitudinal transects (131) were evenly distributed over a tract of mountains of ca. 40 × 200 km. The age of spruces growing at the tree limit and downhill were estimated by annual ring counts. The spruce tree limit had risen (on average by ca. 50 m altitudinally) in ca. 70% of the studied transects as a result of the subsequent growth in height of old, established, formerly stunted individuals. Their growth in height accelerated during the 1930's, in response to the general climatic warming. A rise in the tree limit because of the establishment of new individuals (after 1915) was noted in only 7% of the studied transects. Most of the spruces growing in the tree-limit ecotone established around the 1860's and the 1940's, which were epochs with relatively snowy winters. After 1860, spruce establishment was not correlated with the summer mean temperature. Successful regeneration of spruce at the tree limit is dependent of a deep and stable snow cover and the requisite balance between precipitation–meltwater and evaporation being maintained in the early summer. The importance of air temperatures in May for successful growth and natural regeneration was evident. High air temperature in May is detrimental, since it promotes a too early initiation of growth and a consequent increased risk of frost damage. The spruce populations at the tree limit are recruited both from local seed parents and from long distance dispersal of seed from trees growing at lower altitudes.

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On a étudié l'histoire récente de *Picea abies* (L.) (*Karst.*) à la limite altitudinale des arbes dans la partie médirionale des monts Scandes en Suède. Des transects altitudinaux (131) furent également distribués le long d'une chaîne de montagnes sur environ 40 sur 200 km. L'âge des épinettes croissant à la limite des arbres et à plus basse altitude fut estimé en dénombrant les anneaux annuels. On a trouvé que la limite altitudinale de l'épinette a progressé vers le haut (d'environ 50 m d'altitude en moyenne) dans 70% des transects étudiés, par suite de la croissance subséquente en hauteur d'individus préalablement rabougris. Leur croissance en hauteur s'est accélérée durant les années 1930 à la suite d'un réchauffement général du climat. On n'a noté une élévation de la limite des arbres provoquée par l'établissement de nouveaux individus (après 1915) dans seulement 7% des transects étudiés. La plupart des épinettes croissant à l'écotone de la limite des arbres se sont établis vers les années 1860 et 1940, qui furent des époques où les hivers étaient caractérisés par d'abondantes précipitations neigeuses. Après 1860, l'établissement de l'épinette ne fut plus corrélée avec la température moyenne estivale. La régénération satisfaisante de l'épinette à la limite des arbres est fonction de la présence d'une couverture neigeuse stable et épaisse et d'un équilibre nécessaire entre la précipitation et la fonte de l'eau, d'une part, et l'évaporation, d'autre part, au début de l'été. L'importance des températures de l'air en mai pour assurer une croissance satisfaisante et la régénération naturelle est apparue évidente. Des températures de l'air élevées en mai sont nuisibles puisqu'elles ont pour effet de provoquer une croissance précoce avec des risques accrus de gel. Les populations d'épinettes à la limite des arbres sont issues à la fois de sources parentales locales et d'une dispersion de longue distance des semances provenant d'arbres localisés à plus basse altitude.

[Traduit par la revue]

Introduction

In general, the altitudinal limit of tree growth has, for a long time, been recognized as a climatically controlled phenomenon. However, the detailed underlying mechanism is not yet fully understood (cf. Daubenmire 1954; Wardle 1974, 1981; Tranquillini 1979). A better comprehension of the tree-line concept may be acquired by further studies of the reproductive characteristics of the different tree species (cf. Wardle 1974, 1981; Kullman 1979; Payette 1983). New insight into the details of this relationship has been gained from studies that show a temporal coincidence between recent climatic changes and altitudinal and latitudinal changes in the tree limit in various parts of the world (e.g., Hustich 1948, 1958; Bray 1971; Franklin et al. 1971; Gorchakovsky and Shiyatov 1978; Kullman 1979, 1981, 1983; Payette 1980; Sonesson and Hoogesteger 1983; Morin and Payette 1984; Payette and Filion 1985). However, since the tree limit is formed by different species in different geographical areas, it may be expected that the tree limit is not everywhere controlled by the same factors (cf. Hermes 1955; Hämet-Ahti 1979). The rate of population responses to a particular climatic shift, therefore, is likely to differ considerably according to the life history characteristics of the species involved.

In Scandinavia, the 20th-century tree-limit changes of mountain birch (*Betula pubescens* Ehrh. ssp. *tortuosa* (Ledeb.) Nyman) and Scots pine (*Pinus sylvestris* L.) have already been investigated (Kullman 1979, 1981, 1983). The present paper accounts for an analogous study of Norway spruce (*Picea abies* (L.) Karst.) in the same geographical region.

Compared with birch and pine, spruce is a much later immigrant in Scandinavia (cf. Moe 1970; Tallantire 1972, 1977; Hafsten 1985). A special dimension is thus involved in a study of the recent tree-limit history of spruce. Factors such as migrational lag, progressive soil processes, and interspecific relationships to prior immigrants must also be considered (cf. Davis 1976; Ritchie 1977; Prentice 1983). The old and much-debated question as to whether spruce is still continuously expanding its range westwards in Scandinavia or not remains controversial. Tallantire (1972, 1977) claims that the western natural limit of spruce in Scandinavia is in balance with the 20th-century climatic conditions (cf. Kullman 1986*a*). Prentice (1983) and others, however, do not exclude the possibility that the spruce limit is not in equilibrium with present-day climate.

The aim of this study is to evaluate the change or stability of

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TABLE 1. Mean (±SD) altitude (m ASL) of the TL-75 for spruce, pine, and birch within the study area

Spruce (n = 131)	875±80	830±75	845±65	910±70	870±75
Pine (n = 93)	830±80	770±75	810±80	865±70	840±90
Birch (n = 214)	930±80	895±60	930±60	955±70	920±70

NOTE: Mean values are shown for all the transects together and for those representing the different slope aspects (e.g., north-facing = NNW + N + NNE + NE). All altitude values were rounded off to the nearest 5-m interval. The data for pine and birch are taken from Kullman (1979, 1981). Numbers of transects involved are shown in parentheses.

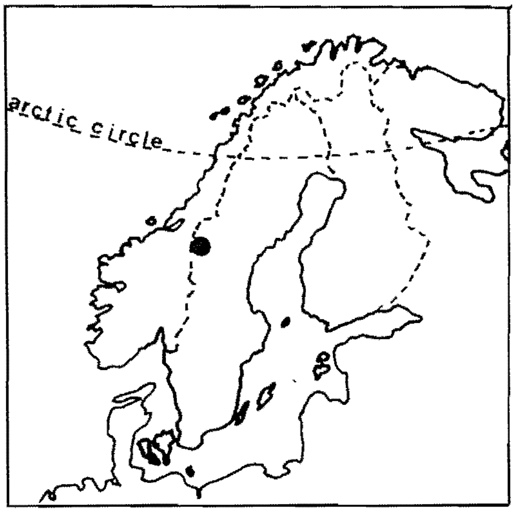

FIG. 1. Location of the study area (●).

the altitudinal spruce tree limit in the recent past. During that time (especially after 1915), a marked thermal amelioration (all seasons) occurred in the Northern Hemisphere (Heino 1978; Ford 1982; Jones et al. 1982; Kelly et al. 1982). The ecological impacts of that and earlier climatic changes are dealt with in particular. The main object of the investigation was the age structure of the spruce populations in the zone below the tree limit. For long-lived, shade-tolerant tree species, such as spruce, the age structure is generally recognized as providing valid information about stand development (cf. Leak 1975; Hett and Loucks 1976; Whipple and Dix 1979; Despain 1983).

Study area

The investigated area (Fig. 1) comprises the southern part of the Scandes mountain chain in Sweden (63°23′–61°53′ N, 13°34′–12°03′ E). It covers the westernmost parts of Jämtland, Härjedalen, and Dalarna areas (ca. 40 × 200 km). Phytogeographically it falls within the Northern Boreal Zone (sensu Ahti et al. 1968).

The physical landscape is characterized by a relatively rounded and smooth relief. The highest massifs rise to 1500–1800 m above sea level (ASL). Gneisses, phyllites, and amphibolite form the bedrock in the northern part, and quartzites, augengneiss, and sparagmites form the bedrock in the central and southern parts of the area. Morainic deposits, glaciofluvial sediments, and lacustrine sediments give rise to local and small-scale landforms.

The area exhibits a marked climatic gradient of local maritimity–continentality from northwest to southeast. The mean air temperature for the months June–August is about 1°C lower in the northwestern compared with the southeastern part. The respective annual temperature amplitude values are 19 and 26°C (1931–1960). The mean annual temperature sum (threshold, +5°C) is 400–500 degree days (mean, 1961–1976) close to the spruce tree limit (Odin et al. 1983). The mean annual precipitation (at 500–600 m above sea level) decreases from 1000 mm or more to 500–600 mm in the same direction.

Man had only a local influence on the altitudinal tree limits in the study area (Kullman 1979, 1981).

Historical forest fires have influenced very few transects of the present study (Kullman 1981).

A varying broad belt of mountain birch (*Betula pubescens* ssp. *tortuosa*) is found just below the alpine zone, succeeded below by montane coniferous forests. In the northern and central part of the study area, spruce is predominant, while the abundance of pine in these forests gradually increases southwards. However, the spruce tree limit is generally higher than that of pine (Table 1). On a more detailed scale, spruce prefers the north- and east-facing slopes and pine prefers the south- and west-facing slopes (Kullman 1986*b*).

The spruce gained at least local dominance at lower altitudes around 3000 years before present (BP). This process was obviously delayed by a millennium or so near the tree limit (Lundqvist 1969; Hafsten and Solem 1976; Tallantire 1977; Hafsten 1985).

The mean altitude of the spruce tree limit within the study area is a little below 900 m ASL. The tree limit rises markedly southwards and eastwards. The highest recorded value is at 1060 m ASL on Mount Sånfjället in the province of Härjedalen. This is the highest known altitude for tree-sized (>2 m high) spruce in Sweden.

A more detailed account of the plant cover and the physiography of the study area can be found in Kullman (1979, 1981).

Methods

The stability of the spruce tree limit was assessed by estimating the ages of all individual spruces growing along 131 transects evenly distributed over the study area. Each transect was 200 m wide and ran perpendicular to the contours of the respective hill slope.

The starting point of each transect was the present-day (around 1975) spruce tree limit (hereafter abbreviated as TL-75). The tree limit was taken as the altitude of the uppermost individual spruce with at least one stem 2 m or more in height. From this altitude, firstly, any spruce (stunted individuals) growing further upslope were located and the altitude recorded (metres ASL), as well as age, height, growth form, vitality, and presence of cones. Secondly, to locate the tree limit of 1915, all the spruces in each transect were scrutinized in the same manner downslope from the TL-75. The altitude at which the uppermost spruce, more than 60 years old (in 1975), at 2 m above the ground, was found, was considered to be the spruce tree limit in 1915 (hereafter abbreviated as TL-15). Single-stemmed spruces with fewer than 60 annual rings at the base were considered to have become established after 1915.

Each transect had a minimum altitudinal extent of 100 m from the TL-75, even in cases where the difference between the TL-75 and TL-15 altitudes was less than this, so that samples of sufficient magnitude could be obtained for making an age-class distribution study.

The basic pattern of the location of the transects was predetermined by the localities where Smith (1920) had recorded the birch tree limit in 1915–1916. These localities were evenly spaced out every 2nd km along a 760 km long meandering route along the forest limit in the mountain valleys. However, spruce does not grow at all these sites. Therefore, a few representative localities were added to provide a geographically more balanced coverage of the study area. All altitudes were measured with a Paulin aneroid barometer (cf. Kullman 1979).

Spruces were aged by taking cores with an increment corer at the root–trunk junction and at 2 m above ground level, along two radii in

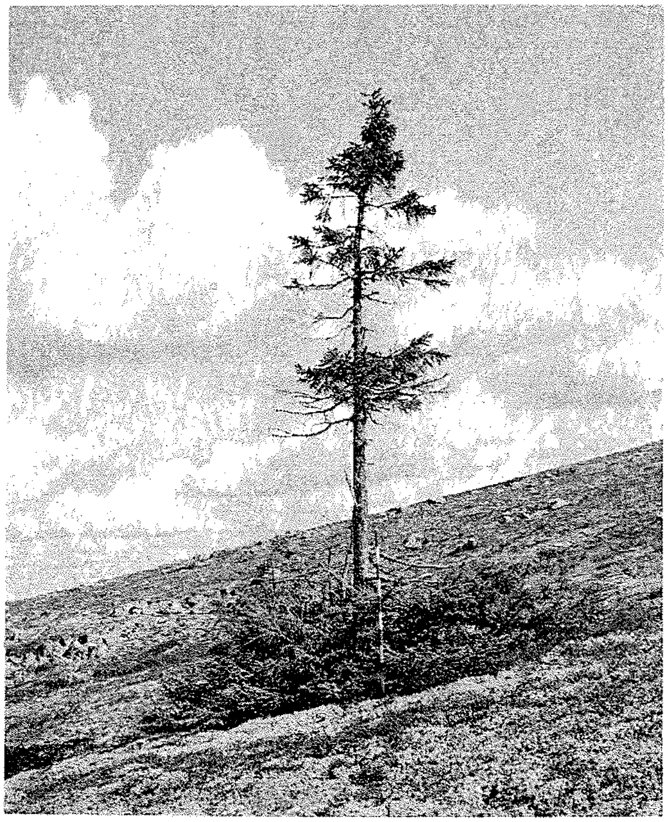

FIG. 2. Single-stemmed spruce at the TL-75 (990 m ASL). This individual became established in the 1860's and was only ca. 1 m high in 1915. The tree bears cones in certain years. The ground cover is made up of lichens and sparse dwarf shrub heath. Mount Sånfjället (Gråsidan), west-facing slope. (Photo: L. Kullman, August 16, 1974.)

each case. Spruces that were less than 2 m in height were sawn off at the root neck and the annual rings were counted on stem cross sections. The annual rings of both the increment cores and the cross sections were counted in the laboratory under a Wild MS stereomicroscope (6–40×). Before counting, both cores and cross sections were soaked in water for a few minutes, pared with a scalpel, and subsequently coated with zinc paste.

Many spruces growing within the transects were multistemmed clones, regenerating by layering of the lowest branches. In these cases, the age of all stems more than 2 m in height was determined and the oldest one was chosen to represent the age of the clone as an individual. However, because the oldest stems of certain of the clones were found to be dead and more or less decayed, their age determination was less accurate. This may have led to a slight bias in the age structure (Fig. 9), the initial (pre-1800) half of which appears to be somewhat too young.

Furthermore, one must bear in mind that for very old spruce growing in northern Scandinavia, annual-ring counts are not absolutely reliable because of missing rings and frost rings (cf. Norokorpi 1979; Zackrisson 1980).

Analyses of height growth were carried out on individual stems at the TL-75. Each of these stems was sawn off at the base and sectioned at 1-dm intervals and the annual rings in each subsample were counted. For all the selected stems the mean age (±SD) for each of the 1-dm levels above ground level was calculated and a picture of the growth in height at different periods of time was obtained.

For each transect the plant cover was documented and the exact location of all spruces present plotted on a sketch.

Results

Zonation of the different tree species

The mean altitude (metres ASL) of the tree limits (TL-75) of spruce, pine, and birch are shown in Table 1. The favourability of south-facing compared with north-facing slopes is clearly indicated. The spruce tree limit, on average, is ca. 50 m higher than that of pine and ca. 50 m below that of birch.

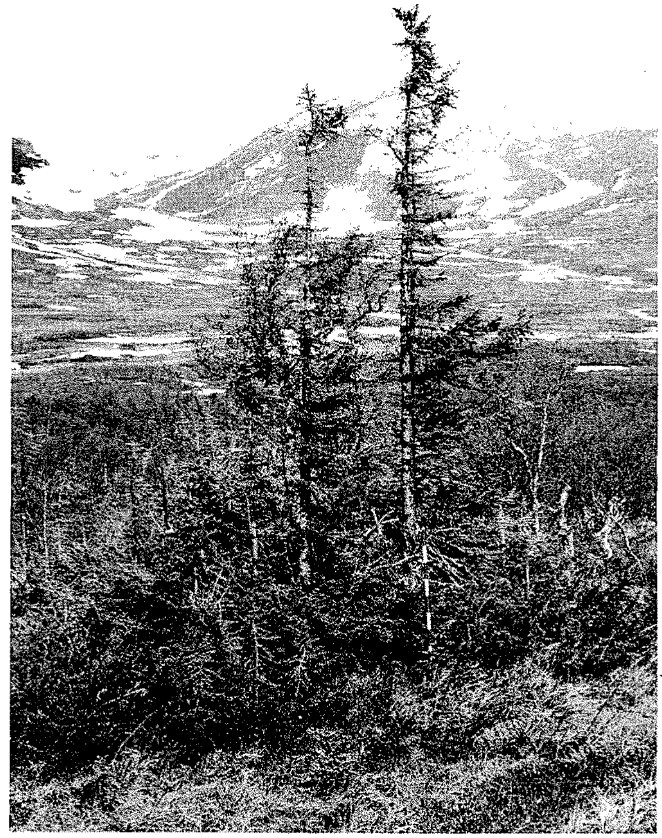

FIG. 3. Spruce clone that in 1915, was growing just above the altitude of the spruce tree limit. In the early 1930's, none of the stems was higher than 1 m. The forest in the background is composed of mountain birch (*Betula pubescens* ssp. *tortuosa*). Mount Stråten, west-facing slope, 750 m ASL. (Photo: L. Kullman, June 10, 1974.)

As defined in this study, the tree limit is by no means everywhere the same as the strict altitudinal limit of the spruce. In fact, a limited number of stunted (<2 m high) spruces were growing above the TL-75 in 48% of all the studied transects (n = 131). The mean (±SD) of the altitudinal difference between the TL-75 and the contemporary absolute altitudinal limit for spruce was 65 ± 50 m. The mean height (±SD) of the stunted individuals growing above the tree limit was 0.84 ± 0.48 m.

Evidence of a rise in the spruce tree limit because of subsequent growth in height

At the majority of all the localities studied (Table A1), there was a zone downhill from TL-75 in which the stems of all spruces present were less than 60 years old (1975) at 2 m above ground level and, in most cases, also more than 60 years old at the root neck. This zone lay above the tree limit in 1915, but the contemporary absolute altitudinal limit of spruce lay at least as high as that of the 1975 tree limit (see Figs. 2 and 3). During the period 1915–1975, old, established, more or less stunted spruces accelerated their growth and exceeded the 2-m limit. In

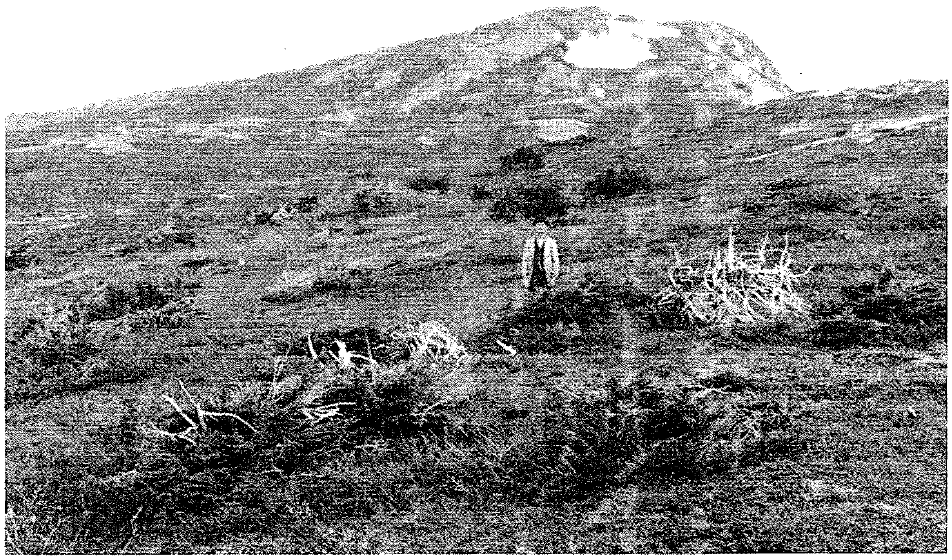

FIG. 4. Stunted population of spruce present above the tree limit. Most individuals established during or before the middle of the 19th century and have subsequently suffered from heavy die-back because of injury caused by the weather. Mt. Mullfjället, south-facing slope, 830 m ASL. (Photo: E. Wibeck, June 20, 1929.)

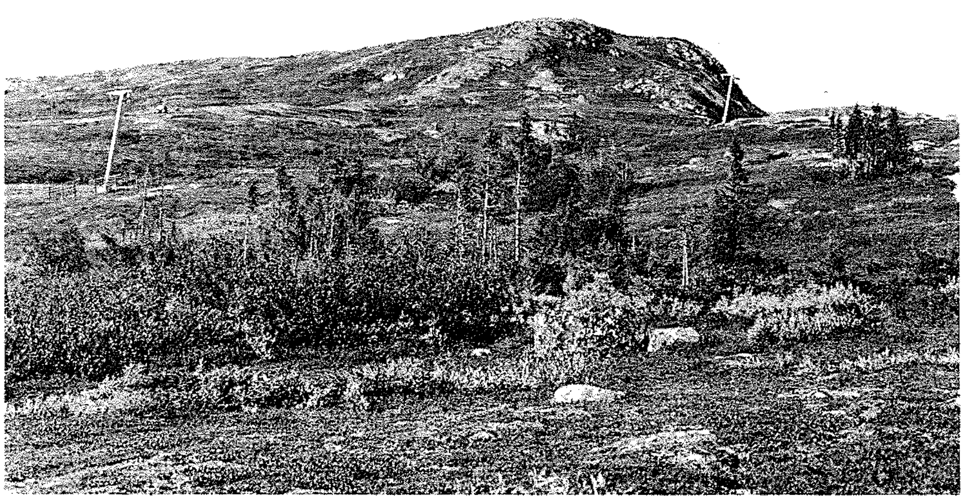

FIG. 5. The same view as in Fig. 4, as seen in 1983. A striking change has occurred in the character of the landscape in the meantime. The old, established, and low-growing spruce have grown into erect trees over 2 m in height and the tree limit has consequently risen. (Photo: L. Kullman, August 6, 1983.)

TABLE 2. Magnitude of the rise in the tree limit as a result of the increased growth in height of old, established individuals, along transects representing the different slope aspects (e.g., N = NNW + N + NNE + NE)

Slope aspect	Mean (±SD) rise in tree limit (m)
N	63±36
E	43±29
S	47±29
W	40±32

NOTE: All values have been rounded off to the nearest metre.

this sense, the tree limit rose in 91 of the 131 transects studied (70%) and remained stable in 40 transects.

No evidence of decayed trees was found in any of the transects that could have suggested that the spruce tree limit has ever been higher than the TL-75.

The mean (±SD) value for this rise in the tree limit (1915–1975) was 47 ± 31 m, almost irrespective of aspects (see Table 2). That the above phenomenon is not simply an artefact is clear from a pair of photographs taken some 50 years apart (Figs. 4 and 5). The physiognomical change in the spruce tree limit ecotone during the 20th century is quite apparent.

Growth analysis of old, established spruces

In each of the transects where the tree limit had risen as a result of subsequent growth in height of formerly stunted individuals (n = 91), one representative stem growing at the TL-75 altitude was selected for analysis of height growth.

The growth examination (Fig. 6) showed that up to about 1930–1940 the growth in height of all 91 trees was slow, but that it increased markedly shortly after that time up to 1965, the last estimated age for the uppermost 10 cm subsample of the stems.

Evidence of tree-limit rise because of establishment of new individuals

At nine (7%) of the localities (Table A2) there is a zone below the TL-75 where all tree-sized individuals are less than 60 years old, estimated at the root neck. Here there has been a genuine altitudinal rise in the tree limit through establishment of new individuals after 1915.

The mean (±SD) value for this altitudinal advance of the tree limit was 31 ± 16 m. Note, however, that in all these cases, only small numbers of tree-sized (mean height, 2.1 m) spruce are involved, all of which germinated between 1921 and 1955, with a peak from 1940 to 1949.

In two of the above cases, the tree-limit advance must have been caused by seed dispersal over a considerable distance. The nearest spruce trees, although not regularly cone bearing, were in both cases ca. 2 km distant. No small, isolated stands of spruce occur any nearer than 6–10 km from the newly established spruce at the tree limit.

Evidence of tree-limit stability

In 24% of the transects, the tree limit had remained stable since 1915 (Table A3). Neither accelerated growth in height of older, previously stunted individuals, nor recent establishment success, had led to a change in the altitude of the spruce tree limit. None of the transects showed any evidence of a lowering of the tree limit.

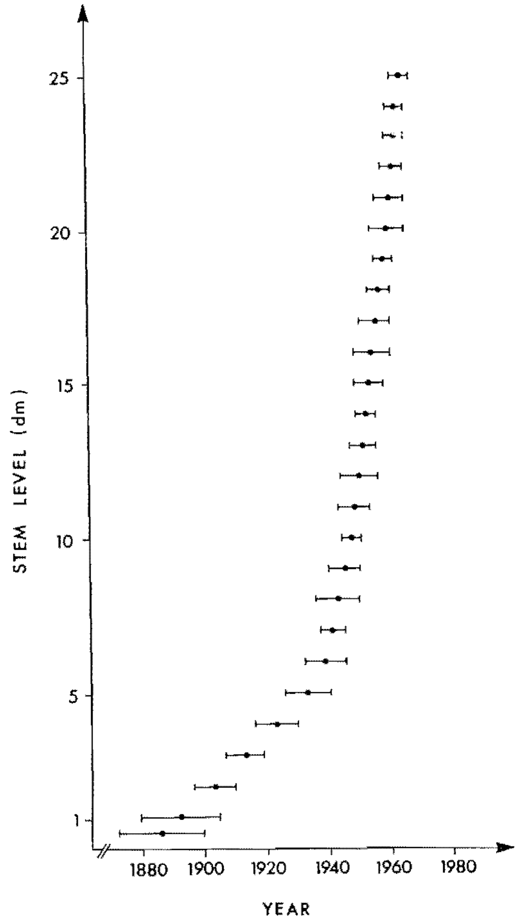

FIG. 6. The mean (±SD) ages of the subsamples of the stems aged at 1-dm intervals above ground level. The trees were selected (one from each site, n = 91) from among those growing at the TL-75 altitude at the sites where the rise in the tree limit was due to the growth in height of old-established trees that were less than 2 m in height in 1915.

Spatial pattern of spruce reproduction (1915–1975)

Altogether, 343 spruces, established after 1915, were found growing within the 131 transects. The young spruces were regularly growing in the proximity of parent trees, all of which were definitely tree sized already in 1915. It is clear from Table 3 that 116 of 343 saplings were found within 10 m of their putative parents and only 32 were found more than 100 m distant (Table 3).

It is obvious that a great proportion of these young spruces (<60 years old at the base) are aggregated around older trees. Nevertheless, beyond 20 m from these putative seed parents, the numbers of young spruces did not fall progressively. Reasonably, this should have been the case if the spruce were derived solely from local seed. This pattern suggests that recruitment to the spruce populations in the transects at the tree limit derives both from local sources and from seed supply from lower altitudes.

Production of cones

The presence of cones could be used as a measure of the possibility of local seed reproduction at different altitudes.

FIG. 7. Even low-growing spruces above the tree limit can occasionally bear cones containing seeds. Mt. Sånfjället (Korpflyet), south-facing slope, 1070 m ASL. (Photo: L. Kullman, August 15, 1973.)

TABLE 3. Numbers of spruce that have become established after 1915 in relation to the distance intervals away from the nearest potential mother tree (i.e., a spruce that was at least 2 m high in 1915)

Interval (m)	No. of spruce
0–10	116
11–20	39
21–30	25
31–40	22
41–50	17
51–60	16
61–70	22
71–80	21
81–90	16
91–100	17
>100	32

NOTE: Data are from a total of 343 spruces growing from the TL-75, 100 m downhill, from all the 131 transects.

Cones were found on trees growing at the TL-75 altitude and 100 m downslope in 42% of the transects. The frequency of cone bearing decreased with altitude. From the TL-75 and 25 m downslope, 33.5% of all transects contained some cone-bearing spruce. Cones were found at the TL-75 altitude on tree-sized spruce in 14% of the transects. In two transects, cones were observed on stunted individuals growing above the TL-75 (Fig. 7).

The mean (±SD) altitudinal limit for cone-bearing trees was 845 ± 85 m. This value is close to the mean altitudinal value found for the uppermost spruces established after 1915 (855 ± 95 m). This relative coincidence of the "cone limit" and the mean upper limit for spruce established after 1915 is probably not simply due to chance.

It is clear from Fig. 9 that the age structure for the spruces (n = 131) constituting the TL-75 is practically identical with the entire population. Thus, it does not seem justified to stratify the age data any further.

The relationship between the numbers of live spruce in the different age-classes and contemporary mean temperature parameters were calculated (Table 4). The number of live spruces in all the decadal age-classes since 1861 (when instrumental records of temperature started in this region) showed a significant negative correlation with the May temperature of the contemporary decade. No correlation with summer or winter temperatures was found.

Discussion

Tree-limit rise

A rise in the tree limit since 1915, brought about by a growth in height, of old, established spruce, was found over the major part of the studied area. This was accentuated towards the end of the 1930–1939 decade, almost exactly coincident with the climax of the 20th-century summer warming (Liljequist 1950; Kelly et al. 1982; Jones et al. 1982). A causal relationship is evident, since apical growth in spruce shows a positive correlation with air temperature (Dahl and Mork 1959; Skre 1972). Lack of weather damage (Fig. 2) is another important prerequisite for net height increment (Langlet 1960). The interpretation in terms of a general climatic change is supported by the fact that the rise was practically irrespective of slope aspect and of the same magnitude as previously recorded for mountain birch and pine (Kullman 1979, 1981).

Spruces continued to grow in height even during the subsequent period of summer temperature decline that was clearly evident after 1950 (Heino 1978; Kelly et al. 1982; Jones

FIG. 8. At their tree limit, spruces are generally found growing in rather open habitats, by preference in dense thickets of the dwarf birch (*Betula nana*). Mt. Rundvalen, east-facing slope, 740 m ASL. (Photo: L. Kullman, June 30, 1973.)

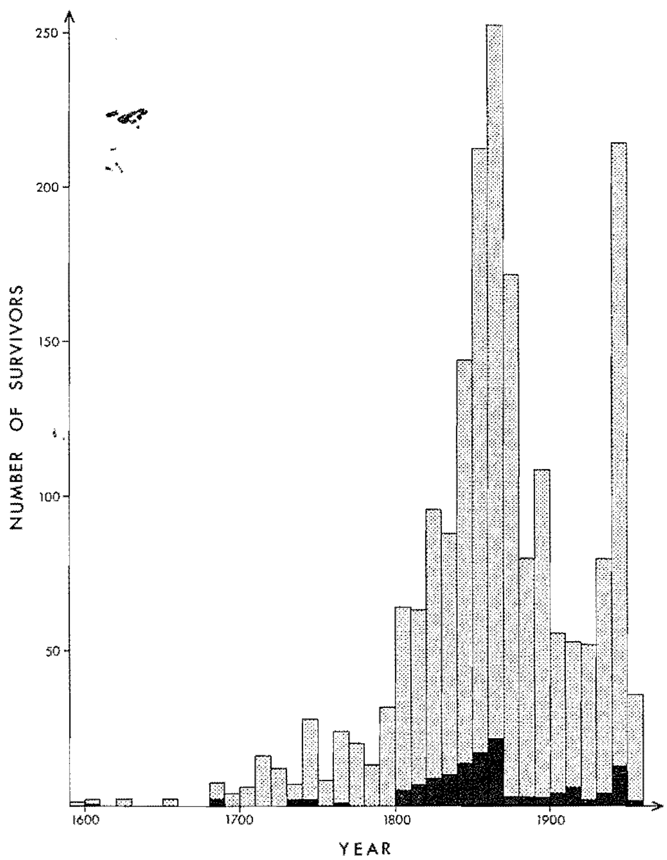

FIG. 9. The age-class distribution (10-year intervals) for the spruce (n = 1958) sampled in all the 131 transects (from the TL-75 altitude and 100 m downhill). Black bars account for the ages of tree-limit individuals, one from each transect (n = 131).

TABLE 4. Relationship between mean number of surviving spruce that became established in all the different 10-year periods (1861–1980) and some contemporary 10-year mean temperature parameters recorded at Östersund (331 m ASL)

Mean temp. for:	Correlation coefficient (r)	Significance
June–Sept.	0.04	NS
June	−0.27	NS
May	−0.48	$p < 0.01$
Jan.–Feb.	0.10	NS

et al. 1982; Eriksson 1982). Thus, the limiting stage of the life cycle occurs at an early age.

Within the tree-limit ecotone, low-growing bushes may develop into trees provided an unbroken period of a few favourable years occurs. This enables them to survive undamaged through a hazardous zone just above the snow cover (cf. Kihlman 1890; Kullman 1981; Holtmeier 1985). Similar observations made on tree growth (*Picea engelmannii*, *Abies lasiocarpa*) by Hansen-Bristow (1981) and Payette et al. (1985) have suggested that in a short-term perspective (average human life), severe periods will not alter the absolute altitudinal species limit. Relatively warm periods promote a rise in the tree limit because of the change from stunted, bushy individuals into tree-sized growth forms. Thus, short-term tree-limit dynamics of species that regenerate vegetatively (Norway spruce included) is more a question of changes in vegetative growth (phenotypic plasticity) rather than one of individual establish-

ment or extinction (cf. Ives and Hansen-Bristow 1983; Kullman 1984).

A genuine rise in the spruce tree limit, i.e., the establishment of new individuals at higher altitudes, has been rare. In this respect, spruce differs radically from both the mountain birch and the pine (Kullman 1979, 1981). This relatively weak natural reproductive response of spruce has been noted in other parts of northern Scandinavia (Mikola 1952; Rubner and Reinhold 1953; Hustich 1958; Blüthgen 1960).

Age structure

Sexual regeneration of spruce was mainly operating during the middle and late 19th century, when a spectacular altitudinal spruce expansion is evidenced (cf. also Kullman 1986*a*). In older geobotanical literature (late 19th and early 20th century), such a process was in fact claimed to be occurring at the altitudinal and latitudinal spruce tree limit in northern Scandinavia (e.g., Nilsson 1897; Holmgren 1904; Aminoff 1907; Frödin 1916). This is also supported by palynological data from the study area, showing a *Picea* peak after 1750 (Lundqvist 1969). On the whole, spruce has increased its altitudinal range more or less continuously during the last ca. 200 years. This process bears a relation to climatic change and is obviously a sequence in the late-Holocene expansion of spruce in Scandinavia. It has recently been suggested by Hafsten (1985) that especially the altitudinal component of the spread of spruce westwards has been considerably delayed.

The general features of the age structure (all the 131 transects taken together) concur, in its earliest part, fairly well with the known historical trends in air temperature and soil humidity in northwestern Europe (Lamb 1982, 1984). A slight net growth in the population from the climax of the cold and wet (snowy) Little Ice Age (late 17th century) to the early part of the 19th century may be a reflection of the thermal recovery (all seasons) (cf. Bray 1971; Kullman 1986*b*). However, the spectacular peaks seen around and shortly after the middle of the 19th century and during the 1940's, which were relatively cold periods (all seasons) in Scandinavia (Liljequist 1950, 1970; Wallén and Ahlmann 1954, Rudloff 1967), suggest that the demands for effective spruce reproduction at the tree limit are not just a simple question of high summer temperatures. The circumstance that few new spruces established during the climax period of the 20th-century warming indicates that too high temperatures reduce the chances of successful regeneration, because of drought (cf. Tallantire 1972, 1977). It is clearly evidenced that the subalpine zone of the study area experienced a substantial drying during this period (Smith 1957). Furthermore, no correlation was found between the numbers of spruce in the different decadal age-classes (1861–1980) and the contemporary mean decadal summer air temperatures (June–September). Thus, the relationship between spruce establishment and climate is a complex one, obviously involving a delicate balance between temperature and soil humidity. It is likely that above a certain threshold value, too high temperatures are unfavourable for establishment (Kullman 1986*b*). It is possible that changed lapse rates of temperature and moisture are causative in this context (cf. Davis et al. 1980).

No correlation between winter temperature and establishment was found. Nevertheless, the most successful periods of establishment, the 1860's and the 1940's, were relatively cold. These periods were also exceptionally snow rich (Forsslund 1924; Rudloff 1967; Ve 1968; data provided by the Swedish Meteorological and Hydrological Institute), which is probably more important. Sufficient snow cover is a very important factor for the success of young seedlings of *Picea abies* close to its tree limit (Skre 1972; Frey 1983). Furthermore, the snow cover was clearly reduced in amount and duration during the climax of the 20th-century climatic amelioration (Hesselberg and Birkeland 1940; Smith 1957; Hoel and Werenskiold 1962), when spruce establishment was insignificant. Snow is obviously the operational ecological factor for spruce at the tree limit. Earlier investigations in the same area have shown that close to the tree limit, spruce stands preferrentially grows in north- and east-facing slopes with a stable and long-lasting snow cover (Kullman 1986*b*). This spatial pattern should logically have a temporal equivalent and the most pronounced regeneration peaks should have a causal relationship to periods with snow accumulation above average.

The above patterns and conclusions accord well with the palynological evidence for the Holocene migration of spruce in Scandinavia. A consistent feature in such studies is that spruce spread especially actively during periods that are postulated, on other evidence, to have been relatively moist (snow rich) and cold (for reviews, see Hafsten et al. 1979; Huntley and Birks 1983).

A significant negative correlation was found between the number of spruces in the different decadal age-classes and the mean air temperature in May. The ground in the timberline ecotone where spruce grows is snow covered (not deep snow, however) and moist enough during May, which indicates that the above bears little relationship with establishment. Instead, the negative relationship may be better explained in terms of a dehardening or early flushing of small seedlings following high temperatures in May (cf. Frey 1983). This is known to promote a dangerously early initiation of growth at a time when the risk of severe frost is still high (Langlet 1960; Dormling 1982). The first part of the 19th century and earlier, which predates the peak of spruce establishment, showed a high frequency of spring frosts in northern Europe (Rudloff 1967). Hjärne (1762) and Zetterstedt (1833) clearly stated that spruce was heavily injured by frost these days. The peak in establishment during the 1940's should be viewed in the light of very few reported observations in Scandinavia of frost injuries to spruce close to the tree limit during the period from 1932 to 1961 (Mork 1968).

Spruce establishment was clearly evident in generally frosty habitats (e.g., open peat lands). Reasonably, this had been impossible if the frost hazard had not diminished. The preferential growth of spruce in dense thickets of *Betula nana* is possibly due to the reduced danger of frost damage to saplings during the growing season (P'yavchenko 1965).

However, the importance of May temperature and frost injuries in connection with the establishment phase (*sensu stricto*) close to the tree limit should not be overemphasized as a primary factor. A reduction in the frost hazard has obviously been most important for the accelerated height growth (see Figs. 4 and 5).

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Appendix

TABLE A1. The altitudes (m ASL) of the spruce tree limit in 1975 (TL-75) and 1915 (TL-15) at all the localities where the rise in tree limit (magnitude indicated) as a result of growth in height of old, established individuals (less than 2 m high in 1915). the coordinates are those of the Swedish National Grid

Locality	Coordinates*		Aspect	TL-75	TL-15	Change
Hästryggarna	70 346	13 169	N	735	695	+40
Larsvalen	70 333	13 155	W	705	695	+10
Tjuvbodklumpen	70 364	13 178	S	785	695	+90
Skurdalsporten	70 326	13 145	N	740	695	+45
Skurdalsporten	70 324	13 141	S	770	695	+75
Skurdalsberget	70 316	13 142	S	785	750	+35
Skurdalshöjden	70 307	13 155	E	755	730	+25
Rekdalshöjden	70 253	13 113	W	805	795	+10
Högåsen	70 261	13 277	SSE	725	695	+30
Rundvalen	70 201	13 164	E	740	690	+50
Rundvalen	70 204	13 153	S	790	760	+30
Blåhammarkläppen	70 126	13 156	W	840	740	+100
Gräslidfjäll	70 165	13 167	N	860	760	+100
Lillhammaren	70 182	13 203	N	805	690	+115
Ingolvberget	70 198	13 265	NE	800	660	+140
Storsnasen	70 176	13 274	E	820	790	+30
N Tväråklumpen	70 152	13 274	E	805	750	+55
N Tväråklumpen	70 142	13 269	SE	765	740	+25
Getryggen	70 133	13 272	E	830	730	+100
Getryggen	70 113	13 261	SE	765	740	+25
Getryggen	70 112	13 255	S	820	770	+50
Lillulvåfjället	70 085	13 280	E	735	725	+10
Laptentjakke	70 072	13 293	W	770	745	+25
Stråten	70 132	13 289	W	770	745	+25
Hårdeggen	70 151	13 311	NW	770	750	+20
Västerån	70 146	13 336	N	800	775	+25
Bunnran	70 147	13 362	N	775	715	+60
Pkt 1242	70 147	13 378	NW	815	725	+90
Järpån	70 148	13 426	N	780	730	+50
Kyrkstenen	70 107	13 571	NE	735	690	+45
Ottfjället	70 139	13 571	NE	735	690	+45
Ottfjället	70 108	13 568	S	915	860	+55
Ottfjället	70 099	13 577	SW	940	870	+70
Ottfjället	70 101	13 554	SW	885	860	+25

TABLE A1. *(concluded)*

Locality	Coordinates*		Aspect	TL-75	TL-15	Change
S Kyrkstensskaftet	70 071	13 489	SE	840	755	+85
Pkt 1011	70 064	13 462	S	895	820	+75
Ö Bunnerstöten	70 066	13 398	S	915	845	+70
Smällhögarna	70 025	13 493	NNE	805	800	+5
Trundfjäll	69 941	13 532	W	880	840	+40
Husvålen	69 764	13 506	SSE	920	855	+65
Husvålen	69 765	13 499	SSW	945	875	+70
Nedre Lillvålen	69 769	13 484	SW	890	860	+30
Dunsjöfjället	69 828	13 447	W	920	905	+15
Dunsjöfjället	69 805	13 450	W	900	880	+20
Vargtjärnstöten	69 807	13 429	SSW	905	865	+40
Stortuvan	69 814	13 406	SSW	895	880	+15
Torkilstöten	69 779	13 425	SE	875	870	+5
Viksjövålen	69 734	13 418	S	910	885	+25
Viksjövålen	69 735	13 434	SE	890	860	+30
Falkvålen	69 667	13 447	NNE	885	820	+65
Hårdängesbäcken	69 648	13 448	N	890	840	+50
Särvvålen	69 644	13 490	W	900	865	+35
Ö Stoljan	69 569	13 512	S	865	845	+20
Ruändan	69 565	13 542	S	930	895	+35
Svartmorhöjden	69 584	13 479	S	890	880	+10
Stor-Axhögen	69 613	13 324	S	815	800	+15
Anåkroken	69 498	13 414	S	1005	965	+40
Anåkroken	69 500	13 408	W	965	940	+25
Gråstöten	69 443	13 401	S	930	910	+20
Ånnfjäll	69 455	13 391	S	970	915	+55
Ånnfjäll	69 465	13 375	SSE	1000	945	+55
Ånnfjäll	69 473	13 375	W	975	900	+75
Ormruet	69 459	13 345	SE	935	905	+30
Ramundberget	69 541	13 244	S	930	880	+50
Kariknallarna	69 512	13 249	E	895	810	+85
Storskarven	69 479	13 245	E	885	830	+55
Lillskarven	69 442	13 252	SE	855	830	+25
Rävvålen	69 426	13 255	SW	935	890	+45
Lillskarven	69 448	13 215	SW	975	845	+130
Funäsdalsberget	69 425	13 320	S	960	950	+10
Hamrafjäll	69 443	13 198	SSE	915	860	+55
Hamrafjäll	69 442	13 183	SW	990	935	+55
Glänvålen	69 548	13 139	SW	910	840	+70
Rödfjället	69 369	13 207	NNE	990	900	+90
Rödfjället	69 339	13 241	S	985	880	+105
Rödfjället	59 337	13 256	E	825	805	+20
Brattriet	69 276	13 235	S	975	960	+15
Högvålen	69 093	13 569	SE	925	905	+20
Högvålen	69 092	13 500	S	935	920	+15
Sånfjället	69 063	13 921	SSE	1060	945	+115
Sånfjället	69 081	13 822	S	1025	980	+45
Sånfjället	69 130	13 935	NE	940	885	+55
Sånfjället	69 095	13 786	W	990	910	+80
Sånfjället	69 085	13 786	SSE	940	925	+15
Jakobshöjden	68 935	13 181	SW	965	885	+80
Huskläppen	68 915	13 192	SW	910	900	+10
Ö Barfredhågna	68 874	13 222	S	955	925	+30
Städjan	68 705	13 462	SW	1040	980	+60
Städjan	68 749	13 455	E	930	905	+25
Nipfjället	68 741	13 435	ESE	965	940	+25
Nipfjället	68 741	13 429	S	980	960	+20

*Swedish National Grid coordinates.

TABLE A2. The altitudes (m ASL) of the spruce tree limit in 1975 (TL-75) and 1915 (TL-15) at all the localities where the rise in tree limit (magnitude indicated) was due to the establishment of new individuals

Locality	Coordinates*		Aspect	TL-75	TL-15	Change
Storulvåfjället	70 105	13 246	N	810	790	+20
Middagsvalen	70 068	13 610	NE	835	805	+30
Middagsvalen	70 067	13 605	W	810	795	+15
Ruändan	69 570	13 566	NW	930	910	+20
Falkvålen	69 605	13 405	S	905	865	+40
Ivarsfjället	69 449	13 445	SSE	960	895	+65
Ormruet	69 466	13 355	NNE	935	910	+25
Grönvålen	69 615	13 145	S	830	810	+20
Hästkläppen	69 538	13 229	N	935	890	+45

*Swedish National Grid coordinates.

TABLE A3. The altitudes (m ASL) of the spruce tree limit (TL-75) at all the localities where the tree limit remained stable during the period from 1915 to 1975, i.e., where neither growth in height of stunted spruce, nor the establishment of new individuals, led to any change in the altitude of the spruce tree limit

Locality	Coordinates*		Aspect	TL-75
Skurdalshöjden	70 301	13 144	S	760
Rekdalshöjden	70 266	13 124	NE	685
Ingolvskalet	70 206	13 249	N	690
Mettjeburretjakke	70 114	13 284	W	840
Middagsvalen	70 062	13 608	SSE	825
Tubbeke	70 058	13 442	SE	825
Trondfjäll	69 957	13 539	N	825
Torkilstöten	69 794	13 424	NE	860
S Gröndörrstöten	69 756	13 395	SE	865
Grönfjället	69 720	13 395	S	815
Särvvålen	69 648	13 495	NW	895
Särvvålen	69 652	13 500	N	880
Gruvvålen	69 608	13 258	SW	905
Vallarfjället	69 608	13 294	W	890
Kappruet	69 532	13 425	WNW	910
Kappruet	69 525	13 446	S	930
Fjälländan	69 456	13 478	S	930
Uggarna–Fjälländan	69 453	13 467	S	895
Röstvålen	69 615	13 243	SSE	790
Grönfjället	69 606	13 149	N	835
Klasberget	69 612	13 181	N	835
Ramundberget	69 549	13 258	E	815
Ramundberget	69 557	13 234	SW	915
Malmagsvålen	69 502	13 133	SW	890
Storvallsruet	69 415	13 252	SSW	885
Svansjökläppen	69 455	13 152	NE	825
Storkläppen	69 433	13 172	NE	875
Svanåkläppen	69 407	13 183	NNE	885
Högvålen	69 093	13 503	SW	915
Städjan	68 717	13 455	WSW	900
Molnet	68 771	13 460	SSE	975

*Swedish National Grid coordinates.